Evaluation of ovulation rate and ovarian phenotype in puberal heifers from a cattle population selected for increased ovulation rate[1,2]

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ABSTRACT: Long-term selection for increased ovulation rate (1984 to 2002) has resulted in a unique ovarian phenotype in the MARC Twinner cattle population. Ovulation rate and frequency of bilateral ovulations were examined by rectal palpation in 29,547 estrous cycles for 3,910 heifers (12 to 18 mo of age) in this population. Bilateral ovulations (one corpus lutuem [CL] on each ovary) were of interest because bilateral twin pregnancies result in decreased dystocia and increased calf survival. Ovulation rate increased linearly at a rate of 0.026 CL per year, and it currently averages 1.48 ± 0.04 CL per estrous cycle. Concurrent with the increase in ovulation rate, the frequency of triplet ovulations increased from 0% to $2.3 \pm 0.8\%$ ($P < 0.001$). Ovulation rate of both the right and left ovary increased equally at a rate of 0.013 CL per year, and mean ovulation rate of the right ovary remained greater than mean ovulation rate of the left ovary throughout the study (0.66 vs. 0.55 ± 0.003 CL per estrous cycle; $P < 0.001$). Although correlations were low, ovulation rate of one ovary was negatively correlated ($P < 0.001$; r = -0.07) with ovulation rate of the same ovary in the previous estrous cycle, but positively correlated ($P < 0.001$; r = 0.13) with the contralateral ovary of the previous estrous cycle. The proportion of bilateral ovulations averaged $55.7 \pm 0.7\%$, a value greater than the predicted 49.5% ($P < 0.001$). In addition to dystocia and retained placenta, triplet pregnancies increase the incidence of pregnancies gestating fetuses of opposite sexes and subsequent incidence of freemartins; thus, selection pressure on ovulation rate may need to be adjusted in the MARC Twinner population. The proportion of bilateral ovulations in the population is greater than expected, and this may be an economically important trait, which will respond to selection and be beneficial for improving bovine reproductive efficiency. Understanding factors controlling the increased functional activity of the right ovary and bilateral ovulations may provide further insights into the mechanisms controlling follicle selection and methods to improve reproductive management of cattle.

Introduction

Reproductive performance has a major effect on profitability for cattle producers. Most reproductive traits are polygenic and lowly heritable in nature, resulting in a slow response to genetic selection. A population of cattle with a natural twinning frequency of 50% has been developed at the U.S. Meat Animal Research Center (Echternkamp and Gregory, 2002). Because the first prerequisite for dizygotic twin births in cattle is the ovulation of two Graafian follicles, ovulation rate in yearling heifers was evaluated as an indirect method of selection and found to be an effective predictor of the ability to produce twin calves (Echternkamp et al., 1990a).

Cattle with increased twinning rates had a greater incidence of dystocia and retained placenta, resulting in decreased calf survival and lengthened postpartum interval (Gregory et al., 1996; Echternkamp and Gregory, 1999a,b). Echternkamp and Gregory (2002) reported that when pregnancies resulted from bilateral ovulations (one corpus luteum [**CL**] on each ovary) in this population, dystocia was decreased by 14%, and calf survival was increased by 10% compared with a unilateral twin pregnancy. Because there is negligible uterine migration of embryos in cattle (Scanlon, 1972), bilateral ovulation is the only venue for physically separating twin calves in utero.

Table 1. Frequency (percent ± SEM) of ovulation rate by birth year in heifers selected for ovulation rate

Birth year	No. of heifers	Ovulation rate			
		1	2	3	4
1984	121	92.8 ± 1.0	7.2 ± 1.0	0.0 ± 0.0	0.0 ± 0.0
1985	132	89.5 ± 1.0	10.4 ± 1.0	0.1 ± 0.1	0.0 ± 0.0
1986	104	88.7 ± 1.1	11.3 ± 1.1	0.0 ± 0.0	0.0 ± 0.0
1987	269	85.3 ± 1.0	14.5 ± 1.0	0.1 ± 0.1	0.0 ± 0.0
1988	308	84.1 ± 1.0	15.3 ± 1.0	0.4 ± 0.1	0.0 ± 0.0
1989	301	84.5 ± 1.0	15.3 ± 1.0	0.04 ± 0.04	0.0 ± 0.0
1990	303	84.4 ± 1.0	15.3 ± 1.0	0.3 ± 0.1	0.0 ± 0.0
1991	333	85.7 ± 1.0	14.3 ± 0.6	0.03 ± 0.03	0.0 ± 0.0
1992	302	83.2 ± 1.0	16.7 ± 1.0	0.12 ± 0.1	0.0 ± 0.0
1993	320	81.6 ± 1.0	18.2 ± 1.0	0.11 ± 0.1	0.0 ± 0.0
1994	308	75.0 ± 1.0	24.0 ± 1.0	1.0 ± 0.2	0.0 ± 0.0
1995	274	79.3 ± 1.0	20.3 ± 1.0	0.3 ± 0.1	0.0 ± 0.0
1996	206	74.1 ± 1.2	25.4 ± 1.2	0.6 ± 0.2	0.0 ± 0.0
1997	168	60.3 ± 1.6	37.2 ± 1.6	2.2 ± 0.5	0.3 ± 0.2
1998	92	54.2 ± 2.1	43.8 ± 2.1	2.0 ± 0.6	0.0 ± 0.0
1999	106	60.1 ± 1.9	38.8 ± 1.9	1.1 ± 0.4	0.0 ± 0.0
2000	96	52.9 ± 2.1	44.6 ± 1.0	4.2 ± 2.1	0.0 ± 0.0
2001	71	55.4 ± 2.5	41.8 ± 2.5	2.5 ± 1.0	0.3 ± 0.3
2002	96	55.2 ± 2.1	42.0 ± 2.0	2.2 ± 1.0	0.5 ± 0.3

Increased understanding of bilateral ovulation might provide information on the intraovarian regulation of follicle selection, thereby providing mechanisms to limit ovulation rate at two follicles per cycle in the Twinner population and improving estrus synchronization methods in all cattle. It was of interest to characterize ovarian phenotypes, including bilateral ovulations, within the herd. The objectives of this study were to evaluate 1) the phenotypic response of ovulation rate to selection over 19 yr; 2) variation in ovulation rate between the left and right ovary; and 3) frequency of bilateral ovulations in heifers selected for increased ovulation rate.

Materials and Methods

Determination of Ovulation Rate and Location

The composition of the foundation herd and history of genetic selection has been reported previously (Gregory et al., 1990, 1997). In 1997, there was a decrease in herd size that resulted in a decreased number of observations per year after that time (Table 1).

Beginning at 12 to 14 mo of age, ovulation rate was evaluated by weekly rectal palpation/ultrasound for 7.6 ± 0.03 consecutive estrous cycles per heifer (range of 4 to 12 consecutive estrous cycles per heifer). This resulted in 29,547 estrous cycles evaluated for 3,910 heifers. The number and location of all CL were recorded and used for the determination of genetic estimates of ovulation rate (i.e., heritability and predicted breeding value; Van Vleck and Gregory, 1996a,b; Gregory et al., 1997). These data (1984 to 2002 birth years) were used in the present study to analyze ovulation rate and location. Within double ovulations, the proportion of bilat-

eral ovulations was calculated as the number of bilateral ovulations divided by the total number of double ovulations during the evaluation estrous cycles, multiplied by 100.

Statistical Analyses

Left and right ovulation rate, total ovulation rate, frequencies of single, double, triple, and quadruple ovulations, and frequency of bilateral ovulations were analyzed using models for repeated measures with the MIXED procedure of SAS (SAS Inst., Inc., Cary, NC). Sources of variation were heifer and birth year. Heifer was used as the repeated variable. Ovulation rate of individual ovaries was analyzed using the GLM procedure of SAS with side, birth year, and the interaction as the independent variables. For single and double ovulations, the proportion of ovarian phenotypes demonstrated by an animal was analyzed using the GLM procedure of SAS with ovarian phenotypes (left, right, or bilateral) as the independent variable. For double ovulations, when the analysis was significant ($P < 0.05$), a mean separation was performed using the Student-Newman-Keuls procedure (Ott, 1988). The analysis of the proportion of observed bilateral ovulations against the expected proportion of bilateral ovulations was performed using χ^2, and the relationship between ovulation rates in consecutive estrous cycles was analyzed by the CORR procedure of SAS.

Results

Ovulation rate in heifers in the MARC Twinner population increased linearly at an average annual rate of 0.026 CL ($P < 0.001$; Figure 1). Ovulation rates of the
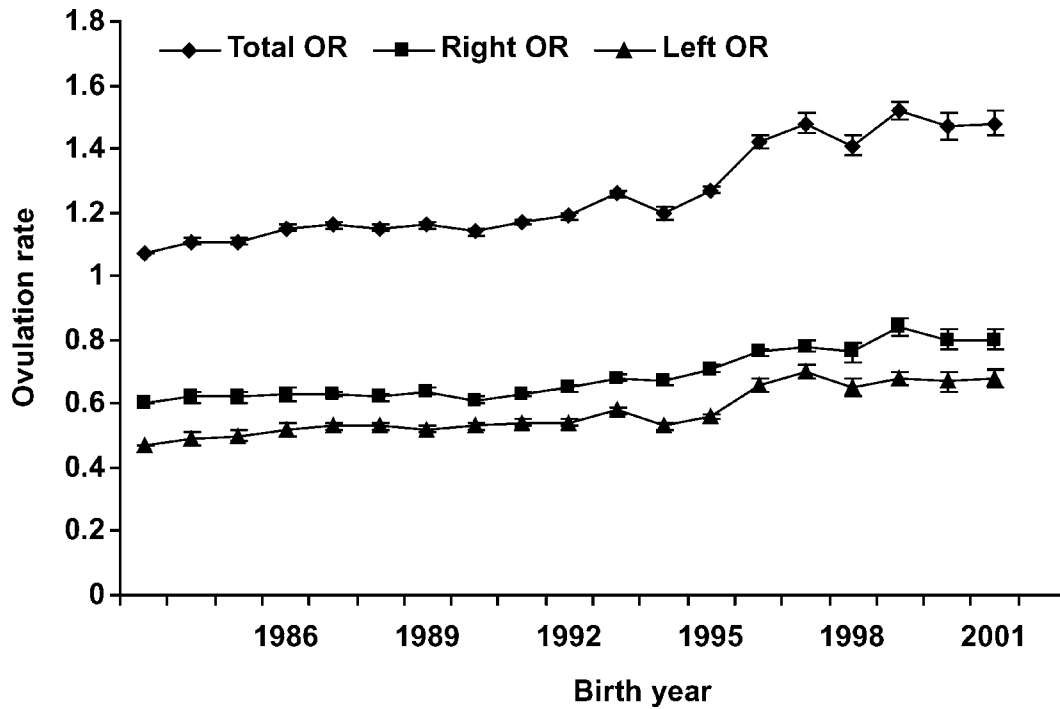
Figure 1. Mean ovulation rate (OR) in heifers selected for multiple ovulations by birth year. Total ovulation rate increased at a rate of 0.026 corpus luteum per year, $P < 0.001$. The number of estrous cycles examined in each birth year is shown in Table 1.

right and left ovaries each increased at an annual rate of 0.013 CL. The ovulation rate for the right ovary was significantly greater than the ovulation rate for the left ovary (0.66 vs. 0.55 $\pm$ 0.003 CL per estrous cycle; $P < 0.001$). The difference between ovulation rate of the right and left ovaries did not change over time; the right ovary averaged 0.11 $\pm$ 0.005 CL more per estrous cycle than the left ovary. Ovulation rate increased linearly at a rate of 0.01 CL per month as heifers increased in age from 12 to 19 mo ($P < 0.01$; data not shown), and this increase was distributed equally between the right and left ovary.

Continued selection for ovulation rate has increased the frequency of double, triple, and quadruple ovulations, concomitant with a decrease in the frequency of single ovulations ($P < 0.001$; Table 1). As in the case of right and left single ovulations, the proportion of right unilateral double ovulations was greater than the proportion of left unilateral double ovulations (Table 2). The proportion of bilateral ovulations within double ovulations fluctuated between 40 and 64%, but it did not change significantly during the course of the study (Table 3). The overall proportion of bilateral ovulations within double ovulations for heifers was 55.7 $\pm$ 0.7%. This was greater (χ^2; $P < 0.001$) than the expected value of 49.5% based on a proportion of 55% right ovulations and 45% left ovulations.

Overall, there was a relatively low positive correlation of 0.219 ($P < 0.001$) between the ovulation rate in two consecutive estrous cycles (Table 4), and the ovulation rate of one ovary was correlated positively

with the ovulation rate of the contralateral ovary in the previous estrous cycle (Table 4). Correlations of ovulation rate with ovulation rate of the same ovary in the previous cycle were −0.083 ($P < 0.001$) and −0.071 ($P < 0.001$) for the left and right ovary, respectively.

Discussion

The Meat Animal Research Center (MARC) Twinner cattle have been selected since 1981 for the ability to

Table 2. Frequency (percent $\pm$ SEM) of ovulation rate by ovarian phenotype in heifers selected for ovulation rate

	No. of corpora lutea		
Class	Left ovary	Right ovary	Frequency
Single	1	0	35.67 $\pm$ 0.28[a]
	0	1	43.96 $\pm$ 0.29[b]
Double	2	0	3.77 $\pm$ 0.11[a]
	0	2	5.03 $\pm$ 0.13[b]
	1	1	10.98 $\pm$ 0.18[c]
Triple	2	1	0.22 $\pm$ 0.03
	1	2	0.18 $\pm$ 0.02
	3	0	0.05 $\pm$ 0.01
	0	3	0.07 $\pm$ 0.01
Quadruple	3	1	0.00 $\pm$ 0.00
	1	3	0.01 $\pm$ 0.01
	2	2	0.01 $\pm$ 0.01

[a,b,c]Within an ovulation class, rows with different superscripts differ, $P < 0.001$.

Table 3. Frequency (percent ± SEM) of bilateral ovulations within double ovulations by birth year in heifers selected for ovulation rate

Birth year	No. of heifers	Bilateral frequency
1984	121	40.0 ± 7.4
1985	132	44.9 ± 5.1
1986	104	43.7 ± 4.9
1987	269	48.2 ± 2.6
1988	308	63.8 ± 2.4
1989	301	63.6 ± 2.4
1990	303	58.4 ± 2.5
1991	333	55.5 ± 2.4
1992	302	53.3 ± 2.4
1993	320	62.8 ± 2.2
1994	308	56.6 ± 2.2
1995	274	60.1 ± 2.7
1996	206	49.1 ± 2.8
1997	168	53.9 ± 2.6
1998	92	58.0 ± 3.2
1999	106	52.4 ± 3.2
2000	96	54.6 ± 3.2
2001	71	52.7 ± 3.9
2002	96	49.2 ± 3.2

produce twin births and since 1985 for the ability to ovulate multiple follicles. The result of this selection pressure for reproductive traits has created a unique population for investigating the molecular mechanisms and genetic variation regulating reproductive function in cattle. Continued selection for ovulation rate and twinning rate has produced an average ovulation rate of 1.48 ± 0.04 CL per estrous cycle in heifers and has resulted in an increased frequency of triple and quadruple ovulations. This suggests that the upper limit of genetic influence on ovulation rate in cattle has not yet been reached in this population. This increase in multiple ovulations provides an excellent model to study ovarian function in cattle, and knowledge gained from this population may be applied to understanding the physiological and genetic mechanisms controlling follicle selection and ovulation in the general cattle population.

Throughout the history of this study, the ovulation rate of the right ovary has been greater than that of the left ovary (Echternkamp et al., 1990a). Increased functional activity of the right ovary compared with the left ovary is well-documented in cattle, and it has been demonstrated in both unselected cattle populations (Reece and Turner, 1938; Rajakoski, 1960) and the MARC Twinner population (Echternkamp et al., 1990a; Echternkamp, 2000; Echternkamp and Gregory, 2002). In the Twinners, this phenomenon occurred either when a single follicle ovulated or when two follicles ovulated from the same ovary, and it could be speculated that this is caused by an increased local temperature due to the proximity of the rumen on the left side.

As has been observed in this population previously (Echternkamp et al., 1990a), ovulation rate was influenced by age of the heifer. Ovulation rate increased as the heifers increased in age during their evaluation estrous cycles. This increase in functional activity of the ovaries with increasing age also has been observed in gilts (Christenson, 1993) and ewes (Schoenian and Burfening, 1990), and it is most likely due to an increase in BW during the evaluation period because maturation of the reproductive endocrine axis is closely linked to growth (Kirkwood and Aherne, 1985; Day and Anderson, 1998).

The positive correlation between ovulation rate from cycle to cycle is to be expected and supports the concept that ovulation rate is a selectable trait. A heifer that has a greater ovulation rate in one cycle is likely to have a greater ovulation rate in a subsequent cycle due to its genetic background. Interestingly, there was a slight negative correlation between ovulation rates of an ovary from one cycle to the next because ovulations tended to occur on the ovary opposite of the previous ovulation site(s). This effect is well-documented with the CL of pregnancy (Saiduddin et al., 1967; Nation et al., 1999; Bridges et al., 2000), and one hypothesis is that local factors involved in the regression of the CL of pregnancy may inhibit development of a dominant follicle (Saiduddin et al., 1967; Spicer et al., 1986; Nation et al., 1999). Therefore, regression of the previous CL in the consecutive cycles examined in the present study may influence the location of the dominant follicle in a subsequent cycle. Given that these correlations are very small, further research will be required to determine whether this is a true effect, and, if so, what factors might be involved.

Although it is interesting to ponder how much ovulation rates could increase in this population with continued selection pressure, the increased incidence of triple and quadruple ovulations is detrimental to the herd. Previous publications (Echternkamp, 1992; Echternkamp and Gregory, 2002) identified the negative association between increased fetal and calf mortality and multiple pregnancies; however, even if triplet and quadruplet pregnancies resulted in live births, the number of replacement heifers would be decreased because of increased numbers of freemartins. Therefore, some selection emphasis on ovulation rate in this herd may need to be replaced with other traits of reproductive importance, such as uterine function, embryonic survival, and live births.

Table 4. Correlation coefficients between ovulation rates (OR) of subsequent cycles[a,b]

| Current cycle | Previous cycle | | |
	Left OR[c]	Right OR[c]	Total OR[c]
Left OR	−0.083	0.139	0.076
Right OR	0.133	−0.071	0.084
Total OR	0.069	0.091	0.219

[a]n = 25,635.
[b]All correlation coefficients were significant, $P < 0.001$.
[c]Left = left ovary; Right = right ovary; Total = total sum of both ovaries.

In the current study, we investigated phenotypic measurements of bilateral ovulation in heifers ovulating two follicles. The overall herd average for proportion of bilateral ovulations within double ovulations was $55.7 \pm 0.7\%$, which is greater than the predicted value of 49.5% (based on a frequency of 55.0% right ovulations and 45.0% left ovulations), suggesting that genetic selection may be possible. There is very little embryonic migration in cattle (Scanlon, 1972), and the embryo remains in the uterine horn ipsilateral to the follicle from which the oocyte ovulated. Echternkamp and Gregory (2002) reported that in the MARC Twinner population, bilateral pregnancies resulted in a lower incidence of dystocia and increased calf survival than unilateral twin pregnancies. Therefore, bilateral ovulation may be a sufficiently economically important trait to be included in the selection criteria for this herd if the genetic parameters can be properly characterized. For selection for bilateral ovulation to be favorable, it must be heritable and preferably have a positive genetic correlation with calf survival. Nonetheless, the heritability estimate for bilateral ovulation will, most likely, be low, as with most reproductive traits, and the genetic correlation between bilateral ovulation and calf survival is yet to be determined.

The physiological mechanisms controlling multiple ovulations have yet to be determined in the MARC Twinner populations. Although no differences in serum FSH concentrations have been detected to date (Echternkamp, 2000; Echternkamp et al., 2004), an increase in serum and follicular fluid IGF-I concentrations suggests a role for this important mediator of gonadotropin action in selection of multiple dominant follicles (Echternkamp et al., 1990b). Furthermore, because serum IGF-I concentrations increase with age in cattle (Jones et al., 1991; Renaville et al., 1993), IGF-I also may play a role in the increase in ovulation rate observed as heifers aged. However, scans for QTL have identified a number of chromosomal regions influencing ovulation rate in the Twinner population (Kappes et al., 2000), and suggest that ovulation rate is under the influence of multiple gene products.

The current study demonstrated that there is a need to further characterize the ovarian phenotype in the MARC Twinner population to better define the components influencing ovulation rate in cattle. Future studies will investigate genes differentially expressed between the left and right ovaries of the MARC Twinner cows to understand the developmental differences that result in increased functional activity of the right ovary and begin to dissect the mechanisms that might be controlling bilateral ovulation. Understanding the factors controlling triple and quadruple ovulations also might provide mechanisms to limit ovulation rate at two.

Implications

Evaluation of the ovarian phenotype in cattle selected for increased ovulation rate confirms there is still much to learn about ovarian function and the physiological and genetic mechanisms controlling follicle selection in cattle. It can be inferred from the deviation of the percentage of bilateral ovulations from the expected value ($55.7 \pm 0.8\%$ vs. 49.5) that selection for this trait may be possible. Additionally, understanding the variation among heifers in the proportion of bilateral ovulations and the mechanisms controlling increased functional activity of the right ovary should provide insights into the biological process of follicle selection. This knowledge would be beneficial for improving reproductive efficiency, including new methods to synchronize estrus and control ovulation rate in general cattle populations.

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